

The Systematics of the Charaxidae (Lepidoptera : Nymphaloidea)

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The family Charaxidae was erected in 1886 by William Doherty for five species of Indian butterfly, namely *Charaxes fabius* (Fabricius), *Ch. kahruba* Moore (= *lunawara* Doherty), *Ch. polyxena hemana* Butler, *Polyura* (not *Eulepis*) *athamas* (Drury) and *P. eudamippus* (Doubleday). The family is listed as Name No. 284 in the *Official List of Family-Group Names in Zoology* (Second Instalment, 1966), but whether or not it should be maintained as a separate family-group of the Rhopalocera is a matter of opinion. Some modern authors (e.g. Aurivillius, 1911; Stichel and Bryk, 1939) have treated the Charaxidae as a subfamily (i.e. "Charaxidinae") of the Nymphalidae (*sensu* Doubleday and Westwood, 1846-52); while others, such as Fruhstorfer and Röber (1916) and Fox *et al.* (1965, *Butterflies of Liberia*), have instead demoted the family to a tribe (i.e., "Charaxidi" or "Charaxini") of the subfamily Nymphalinae (*sensu* Butler, 1869; Kirby, 1871). However, since the Charaxidae differ markedly from the other Nymphaloid families, not only in the early stages and the morphology of the adults but also in their habits in the field (*qq.v.*), I propose to treat them here as a separate family on a par with the Satyridae, Danaidae, Acraeidae, Ithomiidae, and so on, placing them with the latter families in the superfamily Nymphaloidea (which comprises all those butterflies with a suspended pupa, and with only four ambulatory legs in the adults, the forelegs being reduced in both sexes and not used for walking). Alternatively, the Charaxidae can equally well be treated as a separate family of the superfamily Papilionoidea (*s.l.*), in the same way that Klots has done with some of the Nymphaloid families in his *Field Guide to the Butterflies*, 1951.

Doherty, incidentally, was not the first systematist to have separated the Charaxidae from the other Nymphaloid families. Linnaeus (1758, *Systema Naturae*, 10th ed.) for example, instead of placing the two members of the Charaxidae known to him at the time, i.e., *Papilio pyrrhus* (No. 24) and *P. demophon* (No. 36), in his phalanx "Nymphales" to which they rightly belonged, placed them, because of their size and shape, in his "Achivi" (Achaeans) which were a subdivision of his phalanx "Equites" (Knights) to which the Swallowtail butterflies also belonged. Stoll (1782), however, in his essay on the systematics of the butterflies, separated from the latter's "Equites" most of the members of the Charaxidae that he and Cramer had figured and described in their *Papillons Exotiques*, and placed them in his own family "Argonautes" because, as

Note.—Figs. 7-14 will appear next month.

he said, the latter had four ambulatory legs, as opposed to the six that the "Equites" or Swallowtails had; and because, unlike the "Equites", the Argonauts had the abdomen covered below by the hindwings, and veins 2 and 4 of the hindwings typically extended into tails. Jones (1791), who went by the wing-venation chiefly, expressed the opinion that the Argonauts correctly belonged to the Linnean phalanx "Nymphales", with which opinion Fabricius (1793, *Ent. Syst.*, vol. 3) seemed to agree, since he also placed the Argonauts in his own family "Nymphales", together with certain other Nymphalids, Apaturids, and Satyrids, but with *Papilio jasius* L. at the head of it. Latreille (1805, Buffon's *Hist. Nat.*, vol. 14) did much the same as Fabricius, placing *P. jasius* (which he referred to as "*Nymphalis*" *jasius*) at the head of his own "genus" "*Nymphales*" too, the latter taxon not being a genus in the modern sense of the word but rather a superfamily, since he said, on page 82, "Ce genre est divisé en trois grande familles, qui sont les Nymphales proprement dites, les nacrés, les satyres". Shortly afterwards, Fabricius (1807, Illiger's *Mag. Insektenk.*, vol. 6) created a number of new taxa ("Gattungen") for the butterflies, among them being his "genus" *Paphia* (an invalid name, by the way, because it had been used already by Lamarck for a genus of molluscs) which also represented a group of higher rank than a mere genus, since it was subdivided into four sections, two of which contained a number of the Charaxidae, and two some of the larger Limenitids and Nymphalids. Recognising this fact, Ochsenheimer (1816, *Schmett. Europa*, vol. 4) removed *Papilio jasius* from *Paphia*, and placed it instead in his own genus *Charaxes*, thus making *P. jasius* the type-species of the latter by monotypy. Owing, however, to the prior association of *P. jasius* with Latreille's genus *Nymphalis*, it was some time before the name *Charaxes* was generally adopted, such authors as Westwood (1850-2) and Kirby (1871) continuing to refer to *Charaxes* as "*Nymphalis*".

Swainson (1827), the author of the two Nymphaloid families Nymphalidae and Heliconiidae, gave *Paphia* (i.e., *Charaxes* and its allies) as an example of the strong build and powerful flight of certain members of his Nymphalidae, comparing it with the delicate construction and weak flight of the Heliconiidae, and suggested that it should be made a subfamily (i.e. "*Paphiana*") of the Nymphalidae. (But since the latter family has, in recent years, been elevated to superfamily status (i.e. the Nymphaloidea) by some modern systematists, one is now also justified in raising the Charaxidae to family rank, because they are the modern equivalent of the "Paphiana"). Boisduval (1832, 1840), on the basis of the larvae, subdivided his "Penduli" (i.e., those butterflies with a suspended pupa) into Danaides, Nymphalides, Satyrides, Apaturides, Morphides and Libytheides. In his "Apaturides" he placed *Apatura* and *Charaxes*, the larvae of which are smooth, without dorsal scoli, and armed with horns on the head, being unlike the prickly larvae of the typical Nymphalidae. Doubleday and Westwood

(1846-52) maintained most of Boisduval's families, but not his "Apturides" which they lumped, together with numerous unrelated genera, in their family Nymphalidae based on "Nymphalis" *jasius* and other *Charaxes*. Since when, the Charaxidae and the Apturidae have invariably been treated as part and parcel of the Nymphalidae by most authors up to the present day, although these three families actually have very little in common. Now that Hemming (1933, *Entomologist*, vol. 66, p. 225) has fixed *Papilio polychloros* L. as the type-species of *Nymphalis* Kluk (1802) which has priority over *Nymphalis* Latreille, the Nymphalidae no longer primarily represent the Charaxidae but rather the Vanessidae of Butler (1869). If the Nymphalidae are made to include the Charaxidae, the Apturidae, and other Nymphaloid families, it becomes impossible to define, except in the broadest of terms. Of the latter, Barcant (1970, *Butterflies of Trinidad and Tobago*, p. 53) says, "Adequate description of the family as a whole is impossible. It is highly diversified and badly in need of reclassification. It seems to me, for instance, that nothing could possibly justify a common family classification between the tiny flower-seeking Dynamines and the powerful, fruit-sucking Preponas, irrespective of what their body and wing structures may be like. Their habits and habitats are too diverse"

The need for splitting up or subdividing the Nymphalidae or the Nymphalinae of the above authors into smaller and more manageable taxa had, however, been recognised for many years by various authors. For example, Denis and Schieffermüller (1775), in accordance with their dictum, "Ein Aug auf den Schmetterling, das andere auf die Raupe" (one eye to the butterfly, the other to the caterpillar), divided the Nymphaloid butterflies of the Vienna region by the larvae into six families, namely: "Papiliones Nymphales Gemmati" (Satyridae); "P. Versicolores" (Apturidae); "P. Maculato-fasciati" (Limenitididae); "P. Angulati" (Vanessidae); P. Nobiles" (Argynnidae); and "P. Variiegati" (Melitaeidae). No doubt they would have created a family for the Charaxidae, too, if *Charaxes jasius* had occurred in their faunal region! Herrich-Schäffer (1864), this time mainly on the basis of the wing-venation, divided the Nymphaloid genera into Heliconina, Danaina, Brassolina, Biina, Hetaerina, Satyrina (two groups), Elymniina, Ragadina, Eurytelina and Nymphalina. The latter family he subdivided into a number of groups, placing most of the Charaxid genera known to him in his "Protogonius-Agrias" group. Butler (1869, *Cat. Diurn. Lep.*) subdivided the Nymphalinae of Bates (1864, *J. Ent.*) into ten groups, namely: Nymphalides (which contained some of the Neotropical Charaxidae); Apturae (containing *Aptura*, *Charaxes*, and various other Charaxid and Nymphalid genera); Limenitides; Catagrammae; Timetides; Vanessides; Epicaliae; Adoliades; Diadema (in which, oddly enough, he placed the two Charaxid genera *Agrias* and *Godartia*!); and the Argynnides. Doherty

(1886, p. 107) expressed his dissatisfaction with the Nymphalinae of systematists such as Kirby (1871), saying that this family-group presented a confused mass of many genera, the relationships of which *inter se* were extremely vague and uncertain. He suggested that the eggs should be studied with a view to a better understanding of the true relationships of the genera, since the wing-venation, though well and easily defining a particular genus, only very imperfectly expressed the relationship in which it stood to other genera. On the basis of the eggs, Doherty split the Nymphalinae into three families, the Apaturidae, Charaxidae, and the Nymphalidae. His "Apaturidae", however, were based on "*Apatura*" (*Hypolimnas*) *bolina* (which is a Vanessid or Nymphalid, not an Apaturid), and his "Nymphalidae" on "*Nymphalis*" (*Limenitis*) *populi*; hence his "Apaturidae" represented the Nymphalidae in the modern sense, and his "Nymphalidae" the present-day Limenitididae (or Limenitidinae). Doherty was of the opinion that *Charaxes* (which had smooth globular eggs, with obscure ribs and cross lines at the apex only) seemed to connect the Nymphalidae (with their longitudinally ribbed, conical eggs) to the Limenitididae (with their spiky faceted, dome-shaped or rounded eggs).

Clark (1947), however, said the larvae appeared to offer the most dependable basic characters for the primary subdivision of the Nymphaloidea, dividing them into three main groups: (1) those that are spineless and usually fusiform (the Satyridae, Brassolidae, Morphidae and Apaturidae); (2) those that are spiny and cylindrical (the Marpesiidae, Nymphalidae, Ergolidae, Argynnidae and Acraeidae); and (3) those that are cylindrical but provided with "pairs of long fleshy filaments" (comprising the Danaidae). On the basis of the larvae he made the Charaxidae a subfamily of the Apaturidae; but the eggs of *Charaxes*, as already stated above, are globular and smooth with a fluted depression on top, while those of *Apatura* are somewhat conical and longitudinally ribbed (see Frohawk, 1924, *Nat. Hist. Brit. Butts.* pl. 29, fig. 1); so that, on the basis of the eggs at least, the Charaxidae do not belong with the Apaturidae. On the other hand, Ehrlich (1957, 1958), on a comparative study of all "major areas of the integumental anatomy" of the adults of some 300 species of butterflies, made the Charaxidae a subfamily of the Nymphalidae (*s.l.*), giving it equal rank with the Ithomiinae, Danainae, Satyrinae, Nymphalinae, and others. But since many modern authors still maintain family status for most of Ehrlich's subfamilies, it is reasonable to maintain similar rank for the Charaxidae, also. Aurivillius (1911), when he erected his subfamily "Charaxidinae" for the African members of the group, made no attempt to subdivide it into tribes; nor did Ehrlich (1958), who simply said that no tribal division of the Charaxinae was suggested at the time. The main purpose of this paper, therefore, is to try and fill this gap in the systematics of the butterflies, since, to my knowledge, no other author to date

has done so.

Schatz and Röber (1892), on the bases of the early stages and the morphology of the adults, added the following genera to the Charaxidae, originally comprising the two genera *Charaxes* and *Polyura* Billberg: *Euxanthe* Hübner and *Palla* Hübner (both of which are Ethiopian genera), as well as the Oriental genus *Prothoe* Hübner which Semper (1886-92, *Die Schmetterlinge der Philippinischen Inseln*, pp 76-78) had earlier placed in his "Pseudo-Nymphalis" group, adjacent to the "Charaxes" group, of the Nymphalinae (*sensu* Kirby). In addition, Schatz and Röber placed the following Neotropical genera among the Charaxidae: *Siderone* Hübner, *Zaretis* Hübner, *Coenophlebia* Felder and Felder, *Polygrapha* Staudinger, *Prepona* Boisduval, and *Agrias* Doubleday. All the above-named genera they placed in their "Nymphalis" group of the Nymphalidae (*sensu* Doubleday and Westwood). They separated the *Anaea* group of Neotropical Charaxids from their "Nymphalis" group on the basis of the wing-venation, as well as on the larvae which, in the *Anaea* group, are covered with papillae and tubercles, and often have short simple or branched horns on the head. In the latter group they placed *Anaea* Hübner (= *Pyrrhanaea* Schatz), *Hypna* Hübner, and *Consul* Hübner (= *Protogonius* Hübner), all of which Herrich-Schäffer (1864) had grouped together with *Siderone*, *Charaxes*, *Prepona* and *Agrias* in the "Protogonius-Agrias" group of his family "Nymphalina." Reuter (1896), from a detailed study of the palps of the butterflies, also separated the *Anaea* group from the "Nymphalis" group of the Charaxidae, placing the latter in his tribe "Nymphalidi", and the former in his tribe "Anaeidi" (here referred to as the subfamily Anaeinae). However, Fruhstorfer and Röber (1916) recombined these two groups and placed them in their tribe "Charaxidi" Fruhstorfer (1916) added *Anaeomorpha* Rothschild to the list of the New World Charaxidae, and erected the genus *Archaeoprepona* for those species of *Prepona* with black hair-tufts in the hindwings of the males. Fruhstorfer (1913-14) also added *Agatasa* Moore to the list of the Old World Charaxidae, treating it as a subgenus of *Prothoe*. Stichel and Bryk (1939, *Lepidopterorum Catalogus*, parts 91 and 93) maintained Aurivillius's subfamily "Charaxidinae" for all the genera of the Charaxidae, adding to the list the African genus *Hypomelaena* Aurivillius, and the dubious genus *Phyllophasis* Blanchard (= *Sideronidia* Bryk) which is based on *Papilio galanthis* Cramer, known only from the figures in Cramer's *Papillons Exotiques*, 1775. More recently, Comstock (1961), in his monograph on the genus *Anaea*, has lumped together on phylogenetic grounds nearly all the genera comprising the New World Charaxidae (including *Siderone* and *Zaretis*, but not the *Prepona-Agrias* group of species) and has demoted them to subgenera of his "Anaea", and has also resurrected *Memphis* Hübner as a subgenus for a large group of the latter. Be that as it may, *Siderone* and *Zaretis*, should in my opinion,

be separated from the latter's "*Anaea*" group both on the morphology of the adults, and on the larvae which are quite distinctive (*q.v.*). For these reasons they were separated from the *Anaeinae* by Schatz and Röber (1892), and Fruhstorfer and Röber (1916). In this paper I propose to maintain *Siderone* and *Zaretis*, together with *Coenophlebia*, as a separate sub-family of the *Charaxidae*, intermediate between the *Prepona-Agrias* group of species on the one hand, and the *Anaeinae* on the other.

The *Charaxidae* are an outstanding group of medium to large-sized butterflies many of which are scarce in the field, and some are among the most beautiful of all the *Lepidoptera* (e.g. *Agrias claudina sardanapalus* Bates and *Agatasa calydonia* (Hewitson), to mention but two species among others). Most members of this family are robust, fast-flying insects, with a large and deep thorax and a short abdomen. They do not feed at flowers, but will readily come to exuding sap, fermenting fruit, damp and muddy places, and ordure—tastes that they share to some extent with the *Apaturids*. *Charaxes* and (according to Moore, 1899) *Agatasa* have the odd habit (like some *Lycaenids*) of jerking the hindwings up and down in contrary motion when feeding, presumably to distract potential predators from the more vulnerable parts of the body. According to various authors, all the members of the *Charaxidae* have the habit of returning frequently to their feeding places, or if not feeding, to their favourite perches (somewhat in the manner of the *Apaturids*) where the males like to bask in the sun and wait for passing females, defending their territory with great pugnacity against all intruders, particularly other males of the same species. (In Africa I have seen *Charaxes* pursuing birds much larger than themselves on the wing!) The females are more retiring than the males, but will sometimes be seen flying about their foodplants or sunning themselves on a leaf after ovipositing. They are attracted to natural exudates and fermenting fruit like the males, but not to excrement to which the males are especially partial. The females will not tolerate being mobbed by the males while feeding, but will drive them away by striking at them with their powerful wings. The *Charaxidae* have a circum-tropical distribution, being mainly inhabitants of warm rain-forests; but some are found in drier, more open country, while others prefer cooler, montane conditions. Several species occur in the temperate regions, i.e. *Charaxes jasius* in the Mediterranean Subregion, and *Charaxes pelias* Cramer and a few others in the Cape Province of South Africa; while some species of the *Anaeinae* are found north and south of the New World Tropics.

Morphologically, the imagos of the *Charaxidae* differ from those of the other *Nymphaloid* families in having veins 7 and 8 of the forewing generally much longer than their common stalk, with vein 8 curving downwards at its termination. (In *Charaxes* vein 8 ends at the outer margin below the apex of the

wing, but in the *Anaeninae* and some other genera it tends to end at the apex, or in the costa of the forewing basad of the apex). In the Ethiopian *Euxanthe* and *Hypomelaena*, and in the Neotropical *Anaeninae*, there is also a tendency for some of the subcostal veins to anastomose with the costal vein, and in some species the first subcostal vein (vein 11) is vestigial or absent. The antennae of the Charaxidae are gradually thickened to a club, the terminal four or five segments being longer ventrally than dorsally, thus giving the antennae the appearance of being rolled up at the tip. The palps are also distinctive, being, in the main, uniformly wide and strong, and in some genera (e.g. *Charaxes*, *Polyura*, *Siderone*, *Zaretis*) they are somewhat S-shaped and porrect. The relatively long middle segment of the palps (which, for example, is four times the length of the basal segment in *Charaxes*) is densely squamose, being covered with flat scales on its latero-ventral surface, and has a prominent dorsal tuft of long narrow hair-like scales at its distal end. The terminal segment is short, conical, and densely scaled. Reuter (1896), on the basis of the palps, subdivided the Nymphalinae (*sensu* Kirby) into fifteen tribes of which two, i.e. his "Nymphalidi" and "Anaenidi", comprised the present-day Charaxidae. He pointed out that there are differences between the *Anaeninae* and the main body of the Charaxidae in the shape and structure of the sensory patch (Reuter's "Basalfleck") which is located at the base of the inner side of the basal segment of the palps. In the *Anaeninae* the basal patch is variable in shape, being pulled out in its full length and obtusely rounded off or cut off at right angles in *Anaea*, *Hypna* and *Consul*, but is scutiform, or quadrate in shape in typical *Memphis* and *Polygrapha*. In *Charaxes*, *Prepona* and *Siderone*, however, the basal patch extends more distad from the base of the palp, and is somewhat elongate and conical in appearance. In *Prothoe* and *Agatasa* (which Reuter did not study) the basal patch is short, wide and oblong, being perhaps nearest in shape to *Polygrapha* than to any of the other Charaxidae. Reuter considered his "Nymphalidi" (i.e. the main body of the Charaxidae) to be more closely related to the Limenitididae than were the *Anaeninae* which were more evolved than the former. Müller (1886), from a comparative study of the early stages of the Neotropical genera, concluded that the Charaxidae were related to the Limenitididae too. The *Anaeninae*, as well as *Siderone*, *Zaretis* and *Coenophlebia* (which, as I have just said, I am treating as a separate sub-family in this paper) also differ from the other Charaxids in having, as Comstock (1961, p. 4) has pointed out, a short "ambient" vein at the base of the inner margin of the hindwing, this vein being but vestigial in the last three genera. In addition, the Charaxidae can be divided into two main groups according to whether the costa of the forewing is serrated or not. The serrated (prionopterous) group consists of *Charaxes*, *Polyura*, *Euxanthe* and *Palla*, all of which are Old World genera. None of the New World Charaxidae has a serrated

costa, nor have the Oriental *Prothoe* and *Agatasta*. Rothschild and Jordan (1898) made a detailed examination of the morphology of the prionopterous genera. One of the many points they drew attention to was the specialized type of scaling found near the base of the dorsum of the underside of the forewing, which overlaps a similar patch of scaling on the upper side of the humeral lobe of the hindwing when the insects are in flight. This specialized scaling consists of short erect or semi-erect triangular, or elongated conical, scales. In some of the Charaxidae (i.e. *Charaxes*, *Polyura*, *Euxanthe*, *Anaea*, *Polygrapha*, *Cymatogramma* and *Memphis*) these pointed triangular scales extend above vein 1 into space 1b of the forewing, as far as the fold of the wing halfway between veins 1 and 2; but in the rest of the genera (i.e. *Prepona*, *Agrias*, *Prothoe*, *Zaretis*, *Siderone*, *Coenophlebia*, *Palla*, and the two *Anaeine* genera *Consul* and *Hypna*) these specialized scales do not extend above vein 1. In this respect the first group (comprising *Charaxes* and its allies) shows a relationship with the Limenitididae, since in *Limenitis populi* (L.) the specialized triangular scales also extend above vein 1 into space 1b; while the second group (comprising the remainder of the Charaxidae) shows a relationship with the Nymphalidae (s.s.) in which, in *Nymphalis polychloros*, these scales are delimited by vein 1 and do not extend into space 1b. The above observations, therefore, support Doherty's suggestion that the Charaxidae seemed to connect the Nymphalidae with the Limenitididae.

The male genitalia of the Charaxidae are also distinctive, those of *Charaxes*, *Polyura* and *Euxanthe* differing from all the other butterfly genera in having a short broadly-bifid uncus, combined with a very long slender aedeagus, and a large shoe-horn-shaped juxta which is grooved dorsally and which forms a funnel between itself and the gnathos above it (referred to as the "penis-funnel" by Rothschild and Jordan, 1898, pp. 561-563). In the above genera the aedeagus is almost as long as the abdomen and, in cabinet specimens that have been killed by pinching the thorax, it will often be seen to be projecting from the abdomen—a sure diagnostic sign of the latter genera. In the *Anaeinae* one finds, generally, a relatively simple male genital armature, with a simple pointed uncus, and rounded or elongated valves which often have an apical hook, and a somewhat broad and relatively short, unspined aedeagus (see Comstock, 1961, for figures of the male genitalia). The male genitalia of the *Anaeinae*, and also those of *Zaretis*, *Siderone*, *Coenophlebia*, and the Oriental genera *Prothoe* and *Agatasa* (see figs. 35, 36), to a certain extent show a resemblance to some Limenitids (e.g. *Limenitis* and *Adelpha*), in which there is often a simple pointed uncus, and elongated or rounded valves, but the aedeagus of *L. populi* differs from that of the *Anaeinae* in being terminally hooked. In the *Prepona-Agrias* group (see figs. 31-34), however, one meets with a quite different arrangement in the male genitalia,

with the characteristic club-like, or spiky mace-like, subuncal projections, although in appearance the aedeagus is closer to that of the *Anaeinae* than to *Charaxes*. It comes as a surprise to find that the genital armature of *Prepona* (see fig. 33) is very similar to that of *Agrias* (fig. 34), as was noted by Fruhstorfer (1916) who separated *Archaeoprepona* (see fig. 31) from *Prepona* and *Agrias* on these differences, as well as on the colour of the hair-tufts in the hindwings in the males, which are black in *Archaeoprepona* but are yellowish or light-brown in *Prepona* and *Agrias*. The female genitalia of the above genera have not been examined by me, but according to Comstock (1961, p. 7) those of the *Anaeinae* can be used successfully in the separation of the species. The female genitalia of *Charaxes jasius* and *Palla decius* have been figured by Rothschild and Jordan ((1898, pl. 14a).

The early stages of the Charaxidae are characteristic of the family, those of some African species of *Charaxes*, *Euxanthe* and *Palla* having been described and figured in 1926 by van Someren and van Someren, and by van Someren and Rogers (1927-31); while Moore (1880-1, 1893-6) has figured the larvae and pupae of several species occurring in Ceylon and India. Shirozu and Hara (1969) have figured the egg and early stages of *Polyura eudamippus weismanni* Fritze. Müller (1886) has illustrated and described the early stages of a number of the Neotropical species—information that has been added to by d'Almeida (1922), and others. It is of interest that Stoll, as long ago as 1791, figured the larvae and pupae of *Consul fabius* (Cramer), and *Memphis leonida* (Cramer); but it should be mentioned that, owing to a *lapsus calami*, the large spiky, yellow-banded larva, purporting to be of *Papilio odilia* Stoll (see Stoll, 1791, pl. 6, fig. 3C), is that of *Papilio odius* Fabricius which is not a Charaxid, but a Nymphalid or Vanessid! The early stages of *Charaxes jasius* have been known since the end of the 18th century, and were figured by Hübner in 1811 under the name of "*Nymphalis unedonis*" (presumably named after its foodplant, *Arbutus unedo* L.!) in his *Geschichte Europäischer Schmetterlinge* (pl. 23). The early stages of *Prepona omphale guatemalensis* have been figured by Le Moutt (1932), the egg of which (see fig. 27) resembles quite closely that of *Charaxes* (see figs. 15, 16). The egg of *Siderone marthesia nemesis* Bates was stated by Müller (1866) to be almost spherical but flat on top and at the bottom, the apical plane being larger than the basal one, with the former being finely dentate round its edge. Röber (1916) quoted Fassl as saying that the eggs of *Anaea* were "globular, smoothly shelled and of a light colour"; while those of *Hypna*, according to d'Almeida (1922, p. 170), are almost spherical, measuring a little more than 1 mm. in diameter. The eggs of the African genus *Euxanthe* are somewhat similar to those of *Charaxes*, according to van Someren (1926); but the eggs of *Palla ussheri interposita* Jocey and Talbot, according to the same authors (1926, p. 251) "when first deposited are spherical, but very soon become

irregularly depressed on the top just as in eggs of certain Sphingidae”.

The larvae of *Charaxes* (see figs. 2-5, 21, 22) have two pairs of well-developed horns on the head, with two pairs of smaller, vestigial horns in between the longer ones, and a short bifurcate tail, and are closely similar in appearance to those of *Polyura* (figs. 23, 28). (It should be noted, in passing, that the first instar larva of *Charaxes* and *Polyura* possesses horns on the head, which in the case of *Ch. varanes*, according to van Someren and van Someren (1926, p. 335) “are mere tubercles when the larva has just emerged, but they are gradually extruded within the first 12 hours.” In the remaining genera of the Charaxidae, however, the first instar larva is without horns on the head, and only develops them in the second instar, as in the Apaturidae.) The larva of *Euxanthe* (figs. 6, 20) has the lower pair of horns greatly enlarged, extending outwards and upwards, with the central horns reduced in size. (As noted above, these horns are not present in the first instar, but appear in the second stage.) The caterpillars of the above genera, as far as the head-pieces go, resemble to some extent those of the Neotropical Brassolidae. The larva of *Palla* (figs. 1, 1a) is very unusual in appearance, with its single pair of large bifurcate horns on the head, and with the lateral expansion or frill (false carapace) that is chiefly developed in the region of the sixth to eighth segments, and is vaguely reminiscent of the caterpillars of certain Neotropical Charaxids such as *Prepona*, *Siderone*, and others. The caterpillar of *Archaeoprepona demophon* (L.) (see fig. 7), apart from one pair of well-developed horns on its head, has a pair of long caudal appendages. These features are found in the *Agrias-Prepona* group of species too (see figs. 25, 26), but the larva of *Archaeoprepona* is differently shaped, in that it has a false carapace extending along the dorsum from segment 4 to the anal end as in the larvae of *Zaretis* and *Siderone* (see figs. 8-10). The larva of *A. amphimachus* (Fabricius) has been figured by Müller (1886, pl. 14, fig. 6), and is shown with segments 3 and 4 hunched up and produced anteriorly (like those of *Siderone* and *Zaretis* figured here), with a false eye on either side of segment 5, thus giving it a rather fearsome, reptilian look which doubtless serves to intimidate certain predators. *Archaeoprepona* also differs from the *Agrias-Prepona* larvae in having the horns on the head widely separated (figs. 19, 24). The larva of *Zaretis itylus* (Westwood) (see fig. 8) is somewhat like that of *Siderone marthesia* (Cramer) (see fig. 9) and *S. nemesis* (Illiger) (see fig. 10). The latter two species of *Siderone* are considered to be conspecific by some authors, but it can be seen from the caterpillars that they are not. The larvae of *Zaretis* and *Siderone* resemble more closely the *Archaeoprepona-Agrias* species than the *Anaecinae*, but differ from the former in having a pair of spiky terminally-clubbed horns on the head, and no long caudal appendages. The larvae of the *Anaecinae* differ from those of the other

Charaxids in having no horns, or only short ones, on the head. For example, the larva of *Anaea andria* Scudder (figs. 29, 29a) is without horns, and is covered with small papillae and tubercles, and has two pairs of slightly larger tubercles on the vertex. The larva of *Cymatogramma verticordia* (Hübner) (fig. 12) has one pair of short horns on the head, and in appearance seems to be quite close to that of *Anaea phidile* Geyer (fig. 11). Both the latter caterpillars are markedly unlike the bristly, somewhat *Morpho*-like ones of *Memphis porphyrio* (Bates) (fig. 13) and *M. morvus* (Fabricius) (fig. 14), which fact indicates that *Anaea phidile* does not belong to the same genus as the latter two species. The larva of *Consul fabius* (Cramer) which has been figured by Stoll (1791), and Sepp (1852-5), is naked and fusiform, and is covered with papillae and small tubercles, and has a pair of short blunt horns on its head. D'Almeida (1922, pp. 170-174) has described the caterpillar of *Hypna clytemnestra* (Cramer); it is covered with tubercles too, but is unusual in having a long black subdorsal seta on either side of segments 3, 5, 7, 9 and 11 respectively, with hairs projecting from the side of the head and two pairs of large tubercles on the vertex. The larva of *Anaea suprema* Schaus (= *Anaea zikani* Rebel) has been described and figured by Zikan (1921), and is much like the other naked, papillated larvae of the *Anaeinae*, but has a pair of short bifurcate horns on the head. The caterpillars of the *Anaeinae*—unlike those of *Charaxes* and *Prepona*—have a tendency to roll up the edge of a leaf in which they hide during the heat of the day, but, according to Edwards (1868-72), the larva of *Anaea andria*, if placed in a shaded room, seldom rolls up leaves, but feeds at random over the plant, and when at rest simply lies extended on a leaf. The caterpillars of the Charaxidae feed mainly on dicotyledons, but several African species feed on monocots, i.e. the *Charaxes boueti* group on bamboo, *Arundinaria* spp. (Gramineae), and *Ch. jasius epijasius* Reiche and *Ch. castor* (Cramer) on Sorghum (Gramineae).

The pupae, which are suspended by a characteristic cremaster, are typically smooth, stout and rounded, with the abdominal segments compressed into a cone. In appearance they are perhaps nearest to the Danaidae. The heads of the pupae of *Charaxes* are either truncated, rounded, or slightly bifid (figs. 2a, 2b, 3a, 4a, 5b, 5c, 5d), indicating that this genus is a heterogeneous one. The pupa of *Euxanthe* (figs. 6a, 6b) is ventricose and humped dorsally, with the lower part of the wing-cases bulging outwards; while that of *Palla* (figs. 1b, 1c, 1d) is somewhat triangular in shape, being much broader towards the base than at the apex. The chrysalis of the *Agrias-Prepona* species (figs. 7a, 26a) is more elongate than that of the above genera, and has two strong cephalic projections, and in appearance is somewhat reminiscent of certain Apaturids and Limenitids. The pupae of *Zaretis* (fig. 8a) and *Siderone* (figs. 9a, 10a) are squat and stout, and resemble those of *Anaea* (fig. 29b) and *Memphis* (figs. 11a, 14a) all of which are ana-

what *Charaxes*-like in appearance. The pupa of *Consul* (see Stoll, 1791, pl. 2) is also compressed like that of *Anaea*, but has a dorsal hump and a pair of short protuberances on its head; that of *Anaea suprema*, as figured by Zikan (1921, p. 2, figs. 3 and 4), is also broad, stout and gibbous; while that of *Hypna* (fig. 30) is broadly fusiform, humped dorsally, and has a bluntly bifid head. The somewhat deformed pupa of *Cymatogramma*, with its dorsal humps (see fig. 12a), is perhaps nearer to *Hypna* and *Consul* than to the other New World Charaxids, and in this respect supports Westwood's (1850) opinion that *Cymatogramma* was a link between *Consul* and *Hypna* on the one hand, and *Anaea* (including *Memphis*) on the other.

From the foregoing it can be seen that the genera comprising the Charaxidae have in common a smooth globular egg which is flat, or has a fluted depression, on top; and hence these genera belong together in the same family—that is if one accepts Doherty's system of classifying the butterflies by the eggs. However, on the basis of the larvae (already discussed above), the Old World Charaxidae can be subdivided into the following subfamilies: Charaxinae; Euxanthinae *subfam. nov.* (type-genus, *Euxanthe*); and Pallinae *subfam. nov.* (type-genus, *Palla*). I have not seen figured anywhere in the literature the larvae of *Agatasa* or *Prothoe*, but, according to Corbet and Pendlebury (1956, *Butterflies of the Malay Peninsula*, pp. 243-244), the larva of *Prothoe franck* Godart (not *P. franckii* Hübner; *vide* Cowan, 1968, p. 19; 1970, pp. 23, 58) is "pale purple-brown" in colour, with one pair of horns on the head. However, the adults of *Prothoe* and *Agatasa* are morphologically distinct enough from the other Charaxids for them to be given a subfamily of their own, i.e. the Prothoinae *subfam. nov.* (type-genus *Prothoe*). In addition, the New World members of the Charaxidae can be divided into three subfamilies, with the *Archaeoprepona-Agrias* group of species comprising the Preponinae *subfam. nov.* (type-genus, *Prepona*); the *Zaretis-Siderone* group the Zaretidinae *subfam. nov.* (type-genus, *Zaretis*); and the *Anaeinae* a third subfamily, making a total of seven subfamilies for the Charaxidae in all. The differences in the larvae of these subfamilies are, as we have already seen, supported by differences in the pupae to a certain extent, and also, as is to be expected, by differences in the adults, some of which will be given in the key to the subfamilies below. Using a combination of these characters, the seven subfamilies of the Charaxidae can be further subdivided into a number of distinct tribes which will be dealt with below under the various subfamily headings. These subfamilies and tribes are based primarily on the type-species of the type-genera, as given in Hemming (1967) and as amended by Cowan (1968, 1970). The classification of the Charaxidae proposed here, however, can only be regarded as a provisional one, in view of the fact that the early stages of some of the genera (i.e. *Coenophlebia*, *Polygrapha*, *Anaeomorpha* and *Agatasa*) are apparently still unknown. Much more is still

needed to be known about the early stages of the species comprising the Anacinae in particular, before it will be possible to finalize the systematics of the latter group. This lack of knowledge, however, should not preclude one from attempting a classification of the Charaxidae now, but rather it should serve as a spur to fellow lepidopterists to investigate the early stages of those species that are still unknown; nor should one hesitate unduly to use that information which is presently available, else, in the words of Swainson (1827), "months and years pass away, and that knowledge which, if properly used, might have advanced others one step nearer to the Temple of Truth, is suffered to lie useless and unemployed".

Key to the subfamilies of the CHARAXIDAE

- 1 Costa of the forewing serrated 2
- Costa of the forewing not serrated 4
- 2 Palps dark above, with white spots, or a light stripe below; cell of forewing about two-fifths the length of the forewing, or obtusely rounded anteriorly; mid and hind tibiae and tarsi spined above and below; specialized triangular scales near the base of the underside of the dorsum of the forewing extending beyond vein 1 into space 1b; aedeagus long, extending almost the length of the abdomen, supported by a long, dorsally-grooved, juxta; vinculum narrow 3
- Palps dark above and below; cell of forewing about one-third the length of the forewing; mid and hind tibiae and tarsi spined below only; specialized scales on underside of forewing delimited by vein 1, not extending into space 1b; aedeagus relatively short and very spiny, without a prominent juxta; vinculum broad and thick ...

PALLINAE *Subfam. n.*
- 3 Palps relatively short and erect, the middle segment being about three times the length of the basal segment, black in colour with white spots; hindwing rounded, entire; first and second subcostal veins of forewing Vs.11, 10) typically anastomosing with the costal vein (V.12); abdomen in the males longer than the thorax; tarsus of foreleg in the males short and bluntly rounded, about one-quarter the length of the tibia; mid and hind tibiae and tarsi with long spines above and below

EUXANTHINAE *subfam. n.*
- Palps relatively long, S-shaped, porrect, the middle segment being four times the length of the basal segment, dark-coloured above with a light longitudinal stripe below; hindwing angled or tailed; subcostal veins not anastomosing but running free; abdomen in the males usually shorter than the thorax; tarsus of foreleg of the males longer and more slender but slightly shorter than the tibia; spines on legs shorter than in the Euxanthinae CHARAXINAE
- 4 Subcostal veins of forewing typically running free;

- palps quite large and strong, dark above and light-coloured below 5
- The first two or three subcostal veins of the forewing anastomosing with the costal vein, or if running free, the third subcostal vein (V.9) arising distad of the fifth subcostal vein (V.7); palps not so large and strong, unicolorous above and below, or with alternate dark and light longitudinal stripes below ANAEINAE
- 5 Palps erect; third subcostal vein (V.9) ending in apex of forewing; "ambient" vein not present at base of the inner margin of the hindwing; hair-tufts typically present in the hindwings of the males 6
- Palps somewhat S-shaped, porrect; third subcostal vein ending in costa of forewing basad of the apex; "ambient" vein vestigially present at base of the inner margin of the hindwing; hair-tufts not present in the hindwings of the males ZARETIDINAE *subfam. n.*
- 6 Third and fourth subcostal veins (Vs. 9, 8) of forewing running independently of one another, with the third subcostal vein running almost straight to the apex, and the fourth subcostal ending with a downward curve in the termen; hindwing typically rounded; cell of hindwing typically closed; mid and hind tibiae and tarsi typically spined below only PREPONINAE *subfam. n.*
- Third and fourth subcostal veins of forewing running closely together for much of their course, then both veins suddenly bending away from each other, like a pair of bent callipers, before ending in the apex and termen respectively; hindwing produced into a lobe between veins 3 and 4; cell of hindwing open; mid and hind tibiae and tarsi spined above and below PROTHOINAE *subfam. n.*
- (to be continued)

Early stages of some of the Charaxidae

- Fig. 15. Egg of *Charaxes cithaeron* Fld.; approx. $\times 6$.
- Fig. 16. Egg of *Charaxes varanes vologeses* Mab.; $\times 6$
- Fig. 17. Larval head of *Archaeoprepona demophon* (L.); $\times 1\frac{3}{4}$
- Fig. 18. Larval head of *Archaeoprepona licomedes* (Cr.); $\times 1\frac{3}{4}$
- Fig. 19. Larval head of *Prepona laertes* (Hbn.); $\times 1\frac{3}{4}$
- Figs. 17-19 in Miles Moss's coll. B.M. (N.H.).
- Fig. 20. Larval head of *Euxanthe eurinome ansellica* Butl.; $\times 1$
- Fig. 21. Larval head of *Charaxes jasius epijasius* Reich; $\times 1$
- Fig. 22. Larval head of *Ch. varanes vologeses* Mab.; $\times 1$
- Fig. 23. Larval head of *Polyura pyrrhus sempronius* (F.); $\times 1$. In Rothschild coll., B.M.(N.H.).
- Fig. 24. Larval head of *Agrias claudina* (Godt.); slightly enlarged. In Adams Bequest, B.M. (N.H.)
- Fig. 25. Larva of *Prepona laertes* (Hbn.); nat. size. In Miles Moss's coll., B.M.(N.H.).
- Fig. 26. *Agrias claudina* (Godt.); 26, larva; 26a, pupa (nat. size). In Adams Bequest, B.M.(N.H.).

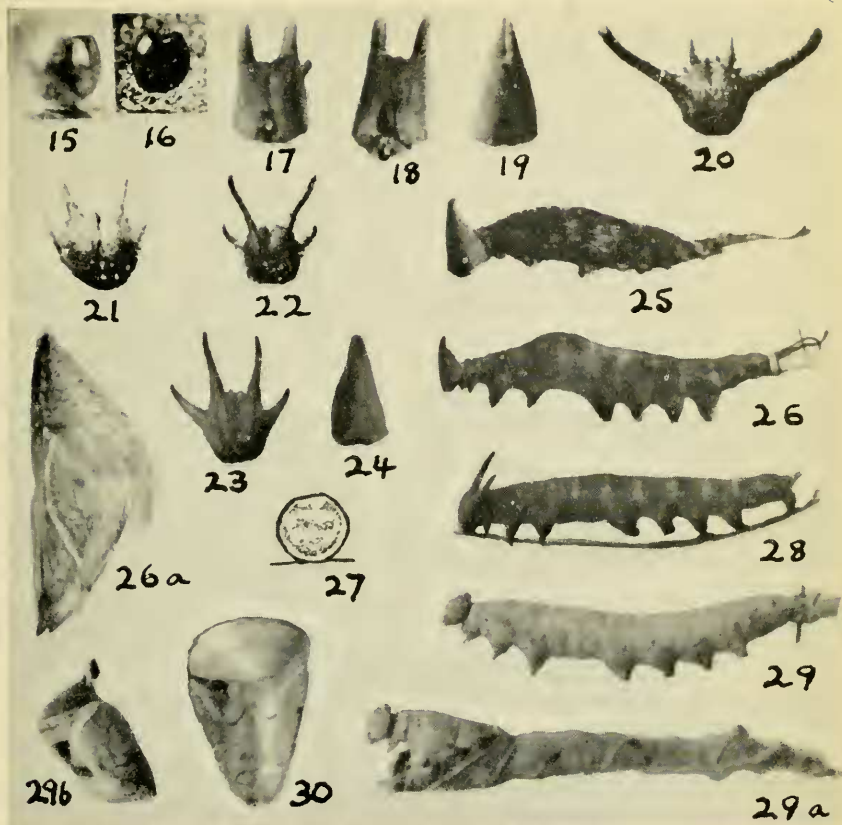


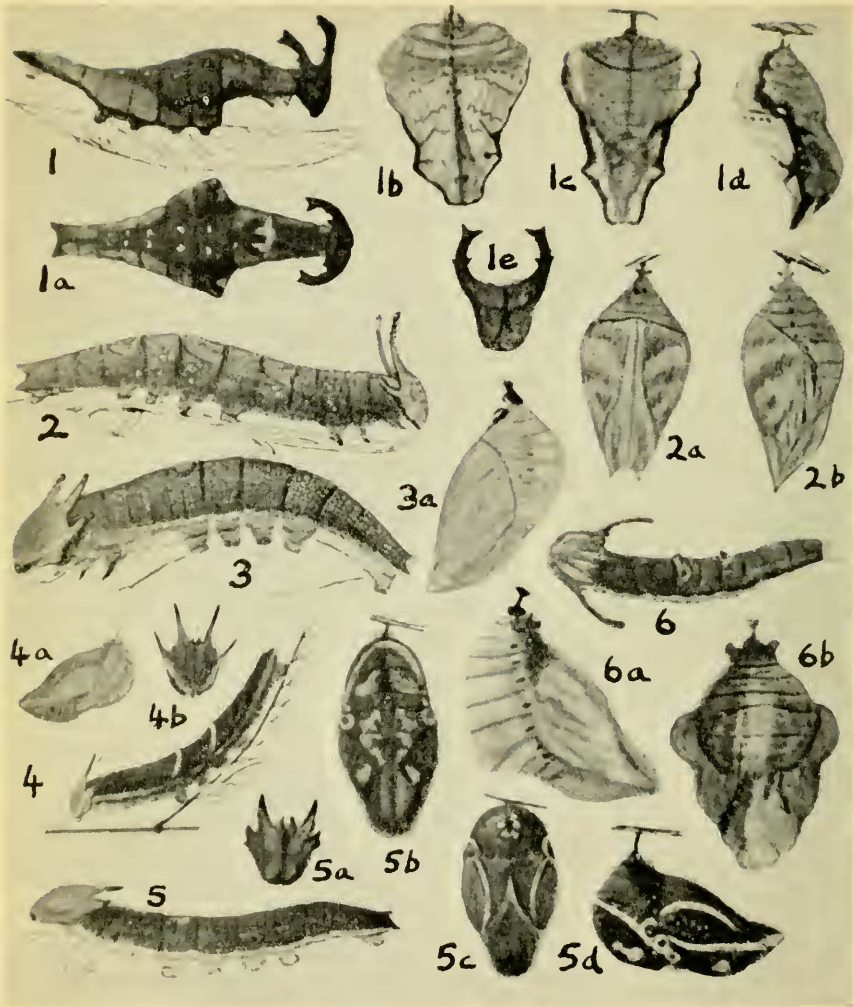
Fig. 27. Egg of *Prepona omphale guatamalensis* Le Moul't (after Le Moul't, 1932).

Fig. 28. Larva of *Polyura pyr'rhus sempronius* (F.); somewhat reduced in size. In Rothschild coll., B.M.(N.H.).

Fig. 29. *Anaea andria* Scudder; 29, 29a, larvae; 29b, pupa. In Rothschild coll., B.M.(N.H.).

Fig. 30. Pupa of *Hypna clytemnestra* (Cr.); dorsal view; nat. size. In Rothschild coll., B.M.(N.H.).

Figs. 15, 16, 20-22 reproduced from photos by V. G. L. van Someren (1926) by courtesy of the Royal Entomological Society of London; figs. 17-19, 23-26, 28-30 photographed by A. H. B. Rydon with the permission of the Trustees of the B.M.(N.H.).



Larvae and pupae of African Charaxidae

Fig. 1. *Palla ussheri interposita* J. and T.; 1, 1a, larva; 1b, 1c, 1d, pupa; 1e, larval head.

Fig. 2. *Charaxes fulvescens monitor* Rothsch.; 2, larva; 2a, 2b, pupa.

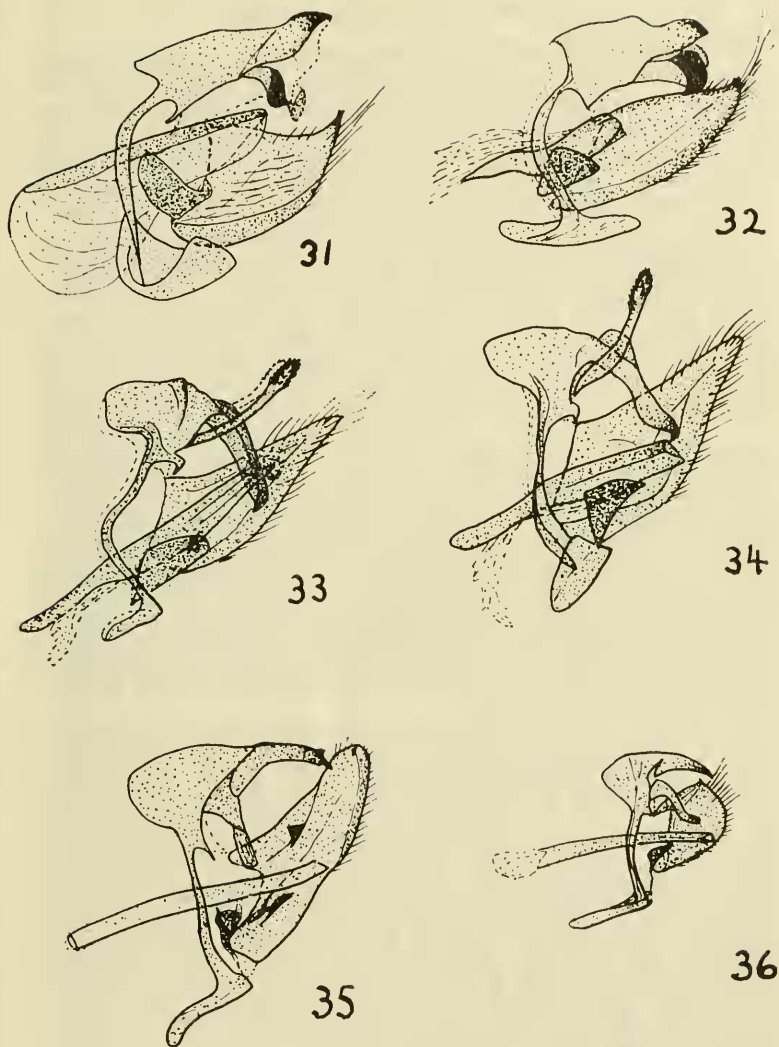
Fig. 3. *Ch. jasius epijasius* Reiche; 3, larva; 3a, pupa.

Fig. 4. *Ch. baumanni* Rogen.; 4, larva; 4a, pupa; 4b, head.

Fig. 5. *Ch. etesipe* (Godt.); 5, larva; 5a, head; 5b, c, d, pupa.

Fig. 6. *Euxanthe eurinome ansellica* Butl.; 6, immature larva; 6a, 6b, pupa.

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Male genitalia of some of the Charaxidae
(The left valve has been removed)

Fig. 31. *Archaeoprepona demophon* (L.); fig. 32, *Nymphalis* (*Prepona*) *chromus* Guér.; fig. 33, *Prepona omphale* (Hbn.); fig. 34, *Agrias claudina* (Godt.); fig. 35, *Agatasa calydonia* (Hew.); fig. 36, *Prothoe franck* (Godt). A. H. B. Rydon del.